

EFFECTS OF VESICULAR-ARBUSCULAR MYCORRHIZAE AND SEED SOURCE ON NURSERY-GROWN BLACK WALNUT SEEDLINGS

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ABSTRACT.—A nursery study was established in Missouri to evaluate the effects of endomycorrhizal inoculation and seed source on the growth of black walnut seedlings. Inoculation, in general, resulted in seedlings with significantly larger sturdiness quotients. *Glomus intraradices* was found to produce larger seedlings than *Glomus etunicatus*, but only differences in height were significant. Seed source affected the quality of seedlings and produced highly significant differences in height and number of first order lateral roots. Inoculation by seed source interactions was significant only for height growth. However, the study clearly demonstrates variation in walnut growth responses with changes in endomycorrhizal symbiont and seed source. Preliminary results indicate that improvement in black walnut seedling quality can occur as a result of inoculating some walnut genotypes with specific endomycorrhizal organisms.

Black walnut (*Juglans nigra* L.) is a valuable timber species that grows extensively throughout the eastern United States. The species is site demanding exhibiting superior growth on deep, fertile, well-drained soils (Fowells 1965). Walnut is managed for both wood and nut production (Garrett and Harper 1999), although trees that exhibit both superior wood and nut production characteristics are uncommon (Rink 1985).

Although black walnut tree improvement began in the early 1960s (Bey 1970), it has recently intensified with the establishment of the Hardwood Tree Improvement and Regeneration Center at Purdue University and a new emphasis on walnut breeding within the University of Missouri Center for Agroforestry (Tourjee and others 1999). Black walnut has also attracted a great deal of "cultural" research in an effort to expedite the initial growth response following outplanting while increasing overall growth and survival.

The effects of vesicular-arbuscular mycorrhizae (VAM) on black walnut have not been extensively studied. However, Melichar and others (1986), Kormanik (1985), Kormanik and others (1982), among others have published research on the

effects of VA mycorrhizae on black walnut growth. The effect of inoculating a variety of black walnut seed sources with different mycorrhizae symbionts and monitoring the walnut genotype/endomycorrhizal interaction in a nursery setting has had limited examination and is the purpose of this work.

The specific objectives of this study were to

- 1) examine nursery growth responses including height, diameter, and number of first order lateral roots > 2 mm of 11 black walnut half-sib families to three endomycorrhizal treatments, and
- 2) determine the significance of the black walnut genotype by *Glomus* genotype interaction in the nursery, especially its effect on the rankings of families among the endomycorrhizal treatments.

STUDY AREA AND DESIGN

The study was installed at the Missouri Department of Conservation, George O. White State forest nursery. The nursery is located approximately 40 km south of Rolla, MO, near Licking, MO. The soil is predominantly Hunting-ton silt loam and contains approximately 45 percent silt, 40 percent sand, and 15 percent clay.

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A randomized split-block design was used in this study. Main plots were endomycorrhizal treatments (3), and sub-plots were black walnut half-sib families (11). Thirty-three treatments, with 45 nuts planted to each treatment, were replicated three times for a total of 4,455 nuts planted.

Three endomycorrhizal treatments,
1) *Glomus intraradices* (Schenck),
2) *G. etunicatus* (Becker & Gerd.), and
3) noninoculated (sterilized sand) were used in this experiment.
Both mycorrhizal symbionts were obtained from Nutri-Link Inc. (Salt Lake City, UT), and shipped in a sand carrier to the University of Missouri. Upon arrival, the inoculum was placed in cold storage until used. The sand for the control treatment was purchased locally and sterilized before used.

Sub-plot treatments consisted of 11 black walnut half-sib families collected from trees in a progeny test located on Hammon's Products Company land near Stockton, MO (table 1). After collection, nuts were hulled, soaked 24 h in water, treated with 5 percent Captan to surface disinfect, placed in large plastic bags according to family, and stored at 2° C to stratify until planting.

The experiment was established at the nursery in late April. One seedbed approximately 85 m in length was utilized for planting. Seedbeds on

each side of the experiment were left fallow, and all three beds were fumigated approximately 3 weeks prior to inoculation and seeding. Each mycorrhizal treatment was assigned at random to one of three main plots in each replication. A 3-m buffer zone was left between inoculum treatments. The inoculum was spread evenly at a rate of 1 L per 6.7 m². The inoculum was then tilled into the seedbed to a depth of approximately 15 cm.

Seed sources were randomly assigned to planting locations within each main plot. Nuts of a particular seed source were placed in the seedbed on a 10.2 x 10.2 cm spacing. A 0.6 x 1.2 m plywood template with drilled holes was used to control spacing. Buffers were not used between seed sources thus allowing spacing comparable to normal operating procedures. Seed sources were separated by a lathe to ensure seed source identification. Each seed source was represented by 45 nuts (5 rows of 9 each) within each main plot. After the sixth week of growth, seedlings were fertilized weekly for 6 weeks with foliar-applied urea at a rate of 13.44 kg/ha.

MEASUREMENTS AND ANALYSES

Seedlings were lifted conventionally in December and measured immediately. Height, diameter, and number of first order lateral roots (> 2 mm in diameter) were recorded for each seedling. A random sample of two seedlings from each treatment in each replication was used to determine the intensity of endomycorrhizal colonization, root volume, root weight, and top weight. Seedlings were severed at the root collar and the root system and top placed in separate bags. Roots were cleared of host cytoplasm using 10 percent KOH, alkaline H₂O₂, and 1 percent HCl then stained with 0.01 percent acid fuchsin-lactic acid solution for mycorrhizal assessment (Kormanik and others 1981).

A 0.5- x 0.5-cm grid was prepared and placed in the bottom of a standard petri dish in which cleared root segments were randomly placed. At each point where a root segment intersected a grid line, a determination was made as to whether or not mycorrhizal structures (either hyphae, vesicles, or arbuscules) were present. One hundred intersection points were observed for mycorrhizal structures. This procedure provides a direct relationship to percentage of lateral roots colonized for a particular seedling.

Seedling tops were dried at 85° C for 48 h and weighed. The root system was divided

Table 1.—Origins of the parent trees of the 11 half-sib black walnut families utilized in the experiment

Family ID #	Parent origin
02	G.O.W. Super Seedling ¹
03	Shannon County, MO
04	G.O.W. Super Seedling
05	G.O.W. Super Seedling
06	G.O.W. Nursery Run Seedling ²
07	G.O.W. Nursery Run Seedling
08	G.O.W. Super Seedling
09	Polk County, MO
10	Cole County, MO
11	Cole County, MO
12	Boone County, MO

¹Large caliper seedlings (> 1.25 cm) of unknown origin taken from the George O. White (G.O.W.) State forest nursery and planted near Stockton, MO in April 1976.

²Nursery run seedlings (< 1.25 cm caliper) taken from the George O. White (G.O.W.) State forest nursery and planted near Stockton, MO in April 1976.

vertically into two equal parts and each half was immersed in a volumetric cylinder to determine water displacement (Burdett 1979). All components of the root system were re-combined, dried at 85° C for 48 h and weighed.

All data were subjected to analysis of variance using the SAS system for personal computers (SAS Institute, Cary, NC). Treatment degrees of freedom were partitioned to perform orthogonal contrasts to compare various treatment combinations (Neter and others 1996). Orthogonal contrasts were used to compare endomycorrhizal treatment means (main plot effect) of the measured seedling attributes. Two degrees of freedom allowed for two planned contrasts. The first contrast compared the effect of inoculation versus no inoculation (control), and the second compared the effect of inoculation with *G. intraradices* versus inoculation with *G. etunicatus*.

RESULTS

Inoculation produced seedlings with a significantly greater ($p < 0.05$) sturdiness quotient than control seedlings (table 2). Sturdiness quotient measures the stocky or spindly condition of seedlings (Thompson 1985), with a high quotient indicating more spindly seedlings.

While not statistically significant ($0.05 < p < 0.10$), inoculation also yielded considerably higher values for height growth, stem weight, colonization percentage, and root volume than noninoculation (table 3). Height growth was the only

measurement for which *G. intraradices* inoculated seedlings was better than *G. etunicatus* inoculated seedlings. With the exception of shoot: root ratio, *G. intraradices* inoculated seedlings had larger mean values for all measured attributes than either *G. etunicatus* inoculated or control seedlings.

The effect of half-sib families (sub-plot effect) on both height growth (table 4) and number of first order lateral roots > 2 mm (table 5) was highly significant ($p < 0.01$). Although family rankings varied with the measurement taken, Family 09 consistently ranked in the top five in all attributes measured with the exception of height, while some families (e.g., 07) ranked consistently low (table 6).

The inoculation treatment by family interaction was statistically significant for height growth ($p < 0.05$) indicating rank and magnitude changes of families in height growth response by inoculation treatment. This interaction was not statistically significant for any of the other traits measured. However, the rankings of the families by each of the treatments were inconsistent within and across all traits measured.

DISCUSSION

A nursery study was established to evaluate the significance of inoculating black walnut seed sources with two species of endomycorrhizal-forming fungi in improving seedling quality. *Glomus intraradices* and *Glomus etunicatus*

Table 2.—Black walnut family sturdiness quotient¹ means and overall treatment and family means of inoculated and noninoculated nursery-grown seedlings

Family	Mycorrhizal treatment and associated sturdiness quotients			Family mean
	Noninoc.	<i>G. intraradices</i>	<i>G. etunicatus</i>	
	Quotients			
02	3.30	4.66	4.94	4.30
03	5.39	7.49	6.62	6.50
04	5.46	5.27	5.91	5.55
05	5.77	6.07	6.40	6.08
06	4.78	5.13	4.41	4.77
07	3.83	6.69	5.58	5.37
08	5.75	6.04	4.46	5.42
09	5.76	4.32	5.33	5.14
10	4.37	3.87	5.79	4.68
11	5.06	6.21	5.08	5.45
12	4.56	7.13	4.88	5.52
Treatment means:	4.91 ²	5.72	5.40	5.34
¹ Sturdiness quotient is ht. (cm) of the seedling divided by the stem diameter (mm). ² Orthogonal contrasts found a significant difference ($P = 0.02$) between treatment means of noninoculated vs. inoculated seedlings. No other significant differences were detected with ANOVA.				

Table 3.—Mean values of all seedling attributes measured in the nursery. Families were subjected to inoculation with *Glomus intraradices* (GI), *Glomus etunicatus* (GE) and sterilized sand (no inoculation (NI)).

Seedling Attribute	Nonin-oculated	<i>Glomus intraradices</i>	<i>Glomus etunicatus</i>	Grand mean
Height (cm)	44.6	45.8	49.6 ¹	46.7
Stem dry weight (g)	5.65	6.51	8.24	6.80
First order lats > 2 mm	3.4	3.6	3.7	3.5
Percentage colonization	33.2	40.9	55.1	43.1
Root dry weight (g)	15.3	19.4	20.5	18.4
Shoot:Root ratio	.473	.432	.452	.452
Root volume (ml)	47.6	55.6	59.1	54.1
Caliper (mm)	8.46	8.67	8.86	8.66
Sturdiness quotient	4.9	5.4	5.7 ²	5.3
¹ Orthogonal contrasts indicated that G.I. inoculated seedlings had heights that were significantly ($0.05 < P < 0.10$) greater than G.E. inoculated and noninoculated seedlings.				
² Orthogonal contrasts indicated that inoculation resulted in seedlings that had significantly ($P = 0.02$) greater sturdiness quotients than noninoculated ones.				

Table 4.—Black walnut family height means and overall treatment and family means of inoculated and noninoculated nursery-grown seedlings

Family	Mycorrhizal treatment and associated mean heights			Family mean
	Noninoc.	<i>G. intraradices</i>	<i>G. etunicatus</i>	
	cm			
02	45.02	42.25	44.79	44.02 ² bcde
03	51.44	52.42	44.96	49.61 abcd
04	40.13	47.84	52.53	46.83 abcde
05	51.00	54.89	44.98	50.29 ab
06	42.62	51.64	40.95	45.07 abcde
07	44.29	51.58	50.57	48.81 abcd
08	53.47	52.26	43.51	50.52 a
09	45.40	41.44	44.48	43.69 cde
10	33.18	42.32	49.56	41.69 e
11	45.30	58.28	46.16	49.92 abc
12	38.91	50.75	40.47	43.38 de
Treatment means:	44.61 ¹	49.61	45.83	46.68
¹ Orthogonal contrasts indicated no significant differences among mycorrhizal treatments.				
² Means sharing the same letter within provenance means are not significantly different at $P < 0.05$ using Duncan's New Multiple Range Test.				

were utilized. Attempts to improve seedling quality through cultural treatments have not led to an agreement on parameter(s) that best correlate with outplanting success. Williams and others (1985), working with walnut reported that geographic seed origin was best correlated with field performance of nursery stock. Thompson (1985), working with conifers, measured a number of seedling parameters that can be used as predictors of outplanting success.

These parameters are either direct seedling measurements or composites of two or more variables. One measurement, sturdiness quotient, was used in our study to determine its' correlation with black walnut outplanting success. Because there is not just one or two seedling parameters that have been demonstrated to be good indicators of field performance in walnut, many other variables were also evaluated.

Table 5.—Black walnut family first order lateral root means and overall treatment and family means of inoculated and noninoculated nursery-grown seedlings

Family	Mycorrhizal treatments and associated mean first order lateral roots > 2 mm.			
	Noninoc.	<i>G. intraradices</i>	<i>G. etunicatus</i>	Family mean
	number of laterals > 2 mm			
02	2.54	3.59	2.33	2.82 ² f
03	3.07	2.23	2.53	2.61 g
04	2.76	2.74	2.04	2.51 g
05	4.37	3.43	3.15	3.65 de
06	3.35	3.48	4.18	3.67 d
07	2.02	1.95	2.28	2.08 h
08	3.66	5.56	7.02	5.21 b
09	5.01	5.10	6.64	5.45 a
10	3.50	6.23	1.89	3.87 c
11	3.42	2.77	4.51	3.57 e
12	<u>3.32</u>	<u>3.16</u>	<u>4.89</u>	<u>3.79</u> cd
Treatment means:	3.36 ¹	3.66	3.57	3.53

¹Orthogonal contrasts indicated no significant differences among mycorrhizal treatments.
²Means sharing the same letter within provenance means are not significantly different at P<0.05 using Duncan's New Multiple Range Test.

Table 6.—Rankings¹ of family means for seedling parameters measured in the nursery

Rank	Root vol.	Ht.	Dia.	Lats > 2mm	Stm. Wt.	Rt. Wt.	% Colon.
	Family						
1	05	08	09	09	05	09	05
2	09	05	08	08	04	11	12
3	11	11	06	10	11	08	08
4	10	03	11	12	08	05	09
5	02	07	02	06	09	02	06
6	08	04	05	05	03	04	10
7	03	06	10	11	02	10	03
8	06	02	03	02	10	03	11
9	04	09	12	03	12	06	07
10	12	12	04	04	07	12	02
11	07	10	07	07	06	07	04

¹All rankings are from highest to lowest means.

Inoculation Effects

A significant response ($p < 0.05$) to mycorrhizae inoculation was observed in sturdiness quotient and near-significant differences ($0.05 < p < 0.1$) were found for height growth, stem weight, percentage colonization, and root volume (table 3). Of the two organisms evaluated, *Glomus intraradices* proved superior to *Glomus etunicatus* when all growth indices were evaluated collectively.

Generally, other studies have shown the same positive effects of inoculation on walnut seedling morphological characteristics that we observed (Schultz and others 1981, Schultz and Kormanik 1982, Kormanik 1985, Melichar and others 1986, Dixon 1988). As in the present study, inoculated seedlings have been found to be larger than their nonmycorrhizal counterparts. Moreover, in each of the studies that have compared the effect of different species of

Glomus, each has shown that no single *Glomus* species consistently produces the largest seedling.

Height, caliper, and number of first order lateral roots > 1 mm and 2 mm are morphological characteristics that are most often measured in the nursery. Also, these characteristics are most often used to correlate nursery stock with outplanting success and subsequent survival and growth. For example, Williams (1965) concluded that black walnut seedlings 0.64 cm or larger in diameter survive and grow best following outplanting.

In the present study and in Dixon's work (1988), a significant or near-significant height response resulted from mycorrhizal inoculation. Dixon (1988) utilized *G. etunicatus* and found it to positively stimulate height growth of seedlings. In studies conducted by Melichar and others (1986), Kormanik (1985), and Schultz and Kormanik (1982) no changes in height resulted from inoculation with various strains of endomycorrhizae. However, none of these researchers utilized either *G. intraradices* or *G. etunicatus*. The significant height response reported by Dixon (1988) and found in the present study, but not found by others, would seem to indicate the importance of the mycorrhizal isolate/walnut genotype interaction.

Changes in height will affect the sturdiness quotient of seedlings when caliper is minimally changed. Because height was significantly affected by inoculation in our study but not caliper (the denominator), inoculation resulted in seedlings with significantly higher sturdiness quotients than was observed without inoculation. Sturdiness quotient has not been included in other black walnut seedling studies; therefore, the optimal quotient is unknown. Moreover, the range of sturdiness quotients (high or low) that signifies good quality seedlings is unknown for black walnut.

Caliper response to mycorrhizal inoculation was not significant in our study. However, *G. intraradices* inoculated seedlings were 4.5 percent larger in caliper than the controls. Moreover, in a follow-up study, inoculation with *G. intraradices* resulted in seedlings that were 10.6 percent larger in diameter than the noninoculated controls (data unpublished). Some variation in caliper response to inoculation also exists in the literature. Kormanik and others (1982) indicated that black walnut seedlings inoculated with *Glomus fasciculatus* and a

mixture of VAM fungi were both 27.8 percent larger in diameter than the controls. Dixon (1988) and Melichar and others (1986) have also reported variations in seedling diameter response depending on the endomycorrhizal organism evaluated.

Although not statistically significant, inoculation resulted in a 7.1 percent increase in the number of first order lateral roots > 2 mm. Variation in lateral root promotion with inoculation has also been reported in the literature. Melichar and others (1986) reported that inoculation with a mixture of *G. microcarpus* and *G. fasciculatus* resulted in a significant increase in lateral root numbers. However, inoculating with *G. microcarpus*, *G. mosseae* or *G. caledonius* did not. Dixon (1988) reported significantly more lateral roots promoted with inoculation, but no differences existed among *Glomus* treatments. Dixon (1988) also found lateral root promotion dependent on walnut genotype.

Stem weight and percentage colonization were affected by inoculation but not significantly. As in the present study, Kormanik (1985) reported that mycorrhizal inoculation had an effect on stem weight and percentage colonization ($0.05 < p < 0.10$). Overall comparisons were not reported by Melichar and others (1986), but significant differences in stem dry weight and percentage colonization did exist among treatments. It is noteworthy that the replication by treatment interaction (error a) approached significance ($p < 0.06$) for percentage colonization in our study suggesting that much unexplained variation was present for percentage colonization. This factor alone may explain why there were no significant differences in percentage colonization found between inoculation treatments.

As is evident from this discussion, the response of walnut to endomycorrhizal inoculation as reported in the literature is highly variable. Even changing sites within a nursery and the corresponding changes in soils along with the changes in weather from year-to-year may serve to increase the variation observed. Kormanik (1985) emphasized the role that phosphorous (P) plays in mycorrhizae research. As P availability increases beyond a threshold value in the soil, the effect of mycorrhizal inoculation on seedling growth responses may decrease. Bray 1 P tests in our study revealed an average of approximately 162 kg of P per ha, which is usually not high enough to inhibit mycorrhizal development. However, variation observed within the treatment bed could account for some of the

differences observed. Sword and Garrett (1994), working with an ectomycorrhizal species, found levels of boron to have an effect on colonization. Black walnut genotype may also have been a factor in the varying response of mycorrhizal organisms.

Seed Source Effects

Seed source was found to be significant for height and number of lateral roots > 2 mm. Dixon (1988) found that provenance was significant for root collar diameter, root weight, leaf area, total root system length, and VAM colonization in his study. Other authors have also demonstrated the importance of provenance selection (Bey 1980, Williams and others 1985).

In our study, only one provenance consistently ranked in the top five for the variables measured, emphasizing the importance of selection in securing fast growing planting stock. Family 09 from a select tree located in Polk County, MO, consistently ranked in the top five for all parameters measured with the exception of height (table 6). Family 09 exhibited a height that was 6.4 percent less than the overall provenance mean. However, this family was 6.1 percent larger in caliper and had 35.3 percent more lateral roots > 2 mm than the overall mean. Moreover, it had consistently higher values than the overall means in all other growth attributes measured. Similarly, Dixon (1988) found that one provenance (out of three tested) ranked first in caliper and lateral root promotion (> 2 mm) and second in height regardless of treatment. Family 04, from a George O. White Nursery super seedling planted near Stockton, MO, consistently ranked near the bottom in all measured parameters.

Treatment * Family Interaction

Height was the only growth parameter that was found to have a significant treatment * family interaction. Dixon (1988) studied the effects of mycorrhizal inoculation on growth and development of three black walnut seed sources. He found that the seed source/mycorrhizal interaction was significant for root collar diameter, root weight, leaf area, total root system length, and percentage colonization. None of the interactions described by Dixon (1988) were found to be significant in our study.

Interactions demonstrate that there are rank changes or changes in the magnitude of response of families to different inoculation treatments. To illustrate this point, families 07, 11, and 12 when inoculated with *G. intraradices*, produced seedlings that were taller

than the controls. However, inoculation of families 02 and 09 with *G. intraradices* resulted in seedlings shorter than the control.

Dixon (1988) evaluated three organisms, *G. margarita*, *G. etunicatus*, and *G. deserticola*, of which only *G. etunicatus* was tested in our study. In contrast to our findings, *G. etunicatus* performed well in Dixon's (1988) greenhouse experiment. However, the response to inoculation depended on the seed source. Dixon's work and the results of our study clearly demonstrate variation in growth response in black walnut with changes in endomycorrhizal symbiont and seed source.

CONCLUSIONS

The following conclusions can be drawn from this study:

- 1) Family growth rankings can change as a result of endomycorrhizal colonization.
- 2) Caution must be exerted when making walnut nursery selections because the best family growth may be a result of a treatment/genotype interaction and not superior genetics alone.
- 3) Further research is needed to determine the value of optimal black walnut/endomycorrhizal symbiont combinations.
- 4) Preliminary results indicate that improvement in black walnut seedling quality can occur as a result of inoculating some walnut genotypes with specific endomycorrhizal organisms.

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